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A 20-million-year relationship between mammalian diversity and primary productivity

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Abstract

At global and regional scales, primary productivity strongly correlates with richness patterns of extant animals across space, suggesting that resource availability and climatic conditions drive patterns of diversity. However, the existence and consistency of such diversity-productivity relationships through geological history is unclear. Here we provide a comprehensive quantitative test of the diversity-productivity relationship for terrestrial large mammals through time across broad temporal and spatial scales. We combine >14,000 occurrences for 690 fossil genera through the Neogene (23-1.8 million years ago) with regional estimates of primary productivity from fossil plant communities in North America and Europe. We show a significant positive diversity-productivity relationship through the 20-million-year record, providing evidence on unprecedented spatial and temporal scales that this relationship is a general pattern in the ecology and paleo-ecology of our planet. Further, we discover that genus richness today does not match the fossil relationship, suggesting that a combination of human impacts and Pleistocene climate variability has modified the 20-million-year ecological relationship by strongly reducing primary productivity and driving many mammalian species into decline or to extinction.

Significance Statement

Our study links diversity dynamics of fossil large mammals through time to primary productivity, i.e. net production of plant biomass. Spatial diversity patterns of terrestrial extant animals are often correlated with present-day primary productivity, but it is unclear whether the relationship holds throughout the geological past. Here, we show that higher primary productivity was consistently associated with higher mammalian diversity throughout the geological period of the Neogene, supporting the hypothesis that energy flow from plants to consumers is a key factor determining the level of biodiversity. Our

comparison of the fossil diversity-productivity relationship to present-day data suggests that human activity and Pleistocene climate change have conspired to dissolve the relationship that has characterized our planet over 20 million years.

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One ubiquitous pattern in ecology is the positive relationship between diversity of terrestrial organisms and primary productivity (1-4). For consumers, this relationship is thought to arise because primary productivity limits energy flow to and total biomass at higher trophic levels (5). Because primary productivity depends largely on climatic conditions (1), and spatial richness patterns of extant species are often strongly correlated with climate at global and continental scales, the productivity hypothesis has been successful in explaining spatial patterns of diversity (1-5). However, the present-day diversity-productivity relationship may not be representative for Earth's history, because present-day conditions have been strongly shaped by human activity (6, 7). Exponential increases in human population size and in biomass of a few domesticated species, such as cattle, pigs, and poultry, have resulted in increasing appropriation of net primary production of biomass (NPP) since the beginning of the Holocene (8, 9). Today, human activity removes up to 30% of the global NPP from natural ecosystems, mostly through harvesting, deforestation, and grazing (10). Increasing human impact and strong glacial-interglacial climate oscillations superimposed on Pleistocene environmental changes have dramatically reduced the number of extant large mammal species (7, 11). Here, we test the diversity-productivity relationship in large mammals by analyzing the Neogene fossil record, which precedes Pleistocene climate change and human dominance of natural ecosystems.

To date, the generality of the terrestrial diversity-productivity relationship over long geological timescales remains elusive. Although temporal changes in terrestrial fossil diversity have been linked to changing productivity and temperature (12-14), the few quantitative analyses to date have been performed at highly disparate spatial scales, either global to continental or for single fossil locations (15-17). The evidence for terrestrial diversity-climate relationships from these studies is equivocal, calling into question the universality of the diversity-productivity relationship. Some of the discrepancies may arise because quantitative studies on large spatial scales have used global paleo-climate reconstructions based on marine records (13, 15, 17), which are unlikely to adequately represent terrestrial climatic conditions. Temperature could also be an indirect or secondary driver of terrestrial diversity, because present-day spatial diversity patterns are often better explained by combinations of proxy variables for energy and water availability than by temperature alone (2-4).

To evaluate the mammalian diversity-productivity relationship through the Neogene, we combine Northern-hemisphere mammalian fossil data for stratigraphic stages covering the Miocene and Pliocene epochs approximately 23 to 1.8 million years ago (mya; see Supplementary Information *SI*, Table S1) with regional terrestrial NPP estimates derived from fossil plant communities (18), covering 23-2.6 mya in Europe and 17-2.6 mya in North America (Fig. 1). Our mammalian dataset contains 14,083 fossil occurrence records for 690 genera (orders Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea) in 1,567 locations, divided into three North American and three European regions (Fig. 1) based on biogeographic history (12, 19). We focus on large terrestrial mammals due to their comparatively well-resolved taxonomy, their high preservation rates, and their well-sampled and comprehensive Neogene fossil record. To account for preservation and spatial sampling biases still present in the record, we estimate regional and continental mammalian γ diversity

on the genus level with a first-order Jackknife approach (20) separately within each global stratigraphic stage and each continent-specific land mammal age or unit (Table S1). Terrestrial NPP is estimated from paleobotanical data accounting for temporal uncertainty, uncertainty of climatic reconstruction, and spatial structure. We evaluate the fossil relationship between NPP and γ diversity through time i) across the two continents and ii) across focal regions. Finally, we compare predictions from this fossil diversity-productivity relationship with observed present-day diversity and NPP, to test whether the Neogene relationship has persisted into the present despite Pleistocene climate change and increasing human impact.

Results and Discussion

The temporal dynamics of mammalian γ diversity, i.e. of the estimated regional diversity of genera, strongly differ between the two continents and across our focal regions (Fig. 2A-H). Miocene γ diversity peaked earlier in North America (stratigraphic stage Burdigalian) than in Europe (Tortonian), a difference which has been linked to earlier drying and cooling in North America (14, 21, 22). In our terrestrial plant datasets, North America shows consistently lower NPP than Europe in the Miocene, but not in the Early Pliocene (Fig. 2J, K). As terrestrial NPP data are only available at the resolution of stratigraphic stages, we use the stage-level mammalian diversity estimates in the following analyses. These stage-level diversity estimates generally track estimates in the more finely resolved land mammal ages (Fig. 2; Pearson's correlation coefficients between diversity estimates for stages and diversity estimates for the contemporary land mammal ages: r=0.701, t=5.29, d.f.=29, $P<0.001$ for continents, r=0.688, t=8.31, d.f.=77, $P<0.001$ for regions), although diversity is elevated in long stratigraphic stages compared to the corresponding land mammal ages (e.g. Tortonian in Europe, Fig. 2B). As diversity estimates may partly reflect temporal turnover of genera

within a stratigraphic stage, we assess the effects of temporal resolution by repeating analyses with the diversity estimates in land mammal ages, averaged within each stage.

Our analyses show a significant positive relationship of fossil mammalian γ diversity with NPP across the continents and stratigraphic stages (Fig. 3A, Table 1). We fit generalized linear mixed-effects models (GLMMs) with Poisson-distributed errors and account for the temporal and spatial data structure through random effects. Further, we account for covariates describing known effects on richness by fitting the area of the region or continent and the duration of the stratigraphic stage as fixed effects. Due to the relatively low availability of paleobotanical locations where the taxonomic composition has been analyzed and NPP could be inferred, the regional analyses are restricted to three focal regions with highest data coverage and best spatial and temporal match of mammalian and paleobotanical locations (Western North America, Western and Eastern Europe; Fig. 1, 2). These regional analyses confirm the continental-scale results (Fig. 3B, Table 1). All patterns reported here are robust to the well-known limitations associated with the analysis of fossil data (6), as we find no or little effect (see *SI* methods) of range-through genera (Fig. S1-S2), diversity estimator algorithm (Fig. S2), location definition (Fig. S3), and temporal resolution (analyses using diversity in land mammal ages, Table S2; different methods of allocating paleobotanical data to stratigraphic stages, Fig. 2J, K). Supplemental simulations based on present-day data indicate that first-order Jackknife estimation performs well in the parameter space likely to be important for our high-quality mammalian fossil record (Fig. S4). We also estimate fossil NPP taking climatic uncertainty into account (Fig. S5) and validate the NPP model through comparisons with present-day data (Fig. S6).

Our results provide strong support for the hypothesis that the terrestrial diversity-productivity relationship is a general pattern in ecology and paleo-ecology that persists in time and in space, at least in the Neogene across the two continents analyzed here. Our study might

reconcile previous large-scale paleontological studies, e.g. those reporting that North American diversity of mammals is not consistently related to global temperature through the Cenozoic (15), even though major transitions between evolutionary faunas match periods of climate change in the same region (17, 22). This inconsistency, combined with the significant diversity-productivity relationship found here, could suggest that primary productivity is a more important or more direct driver of terrestrial mammalian diversity than temperature (3), although we do not directly compare temperature and productivity effects. In addition, the plant records in our study recovered regional variation in terrestrial NPP that could not be captured by the single global temperature curve from marine isotope data used in previous work, even though the terrestrial records have patchy spatial coverage and lower temporal resolution (18).

Next, we visually compare whether present-day diversity and NPP estimates were in agreement with the Neogene diversity-productivity relationship. We observe that present-day genus richness of large mammals in North America and Europe falls far below the predictions from the fossil relationship that has prevailed over 15-20 million years (Fig. 3, grey symbols). Additionally, adjusting present-day values for both human appropriation of NPP (Fig. 3, blue symbols) and end-Pleistocene and Holocene extinctions (red symbols) would seem to reconcile present-day values with the fossil relationship, suggesting that increasing human appropriation of NPP (8-10) and the end-Pleistocene and Holocene extinctions (11, 23) have impacted the temporal diversity-productivity relationship in large mammals since the end of the Neogene. However, conclusions from these comparisons have to be taken cautiously. We could not fit a combined model across fossil and present-day data points due to substantial differences particularly in the underlying timescale: the average stratigraphic stage in the Neogene lasted 2.6 million years, whereas the present-day data are a snapshot of the last 10,000 years at most. The large differences in diversity and NPP between

fossil and present-day data could be a result of this differing timescale, and mean that present-day data have to be compared to fossil model predictions that are made outside the range of diversity and NPP values ever recorded in the Neogene (the dashed line in Fig. 3). Nevertheless, we observe that the differences between the fossil diversity-productivity relationship and the observed present-day data points are striking (Fig. 3), and might reflect a fundamental change to the diversity-productivity relationship that occurred between the Neogene and today.

If the diversity-productivity relationship has been changed since the Neogene, we would expect the present-day relationship in space to be weakest in those regions most impacted by climatic oscillations and mammalian extinctions, such as North America and Europe. Across the globe, we find a significant present-day spatial relationship of mammalian diversity with terrestrial NPP (adjusted for human appropriation; see *SI* methods and Fig. S7), in agreement with previous studies (2-4). In contrast, we show that the present-day spatial relationship within the focal regions Western North America, Western Europe, and Eastern Europe is much weaker (Fig. S7), as could be expected due to climatic and anthropogenic impacts since the end of the Pliocene. Presumably, increasing NPP appropriation by human activities in these regions has prevented a recovery from the numerous mammalian declines and extinctions that occurred in the Pleistocene and Holocene and are ongoing (8, 9), which has changed the diversity-productivity relationship through time. These results could be specific to large mammals, because they have been most strongly affected by past extinctions and experience high extinction risk today (7, 24). The applicability of our fossil and present-day diversity-productivity relationships to small mammals is unclear, because small mammals may be less susceptible to climate oscillations and have experienced fewer end-Pleistocene and Holocene extinctions (7, 13). Future studies could test the prediction that the diversity-

productivity relationship through time is consistent with present-day patterns in other taxa, including those less affected by climate oscillations and human impact.

Due to the large spatial and temporal scales of our diversity-productivity analysis, we cannot fully disentangle the ultimate underlying ecological and evolutionary mechanisms: because resources drive consumer abundances and biomass, productivity could directly limit the diversity that can exist in a given region, or it could influence extinction and speciation processes (5, 25). It is clear from our fossil results that productivity is not the only factor influencing diversity, and that mammalian diversity does not perfectly track it through time. In our Neogene models, the effects of area are stronger than the effects of productivity, and the duration of the stratigraphic stage is also a significant covariate in most models. Additionally, there is a surprisingly large amount of scatter in the global present-day diversity-productivity relationship (Fig. S7). Presumably, our Neogene relationship captures the large-scale temporal transition from tropical and subtropical wet environments to much drier and colder temperate systems today (14), rather than a fine-scale temporal correlation between diversity and productivity. Also, the variability in primary productivity might have a cumulative effect, so that regions with stable paleo-climatic history accumulate high diversity over long timespans (26). Although we did not test this explicitly, the weak spatial diversity-productivity relationship in our focal regions today in comparison to the stronger global spatial relationship could support this idea, because the focal regions were influenced by glaciations until relatively recently.

Conclusions

There has been increasing interest in reconciling paleontological and neontological perspectives on diversity (27), but this integration has been challenging due to the inherent

differences in sampling, timescale, and taxonomy (6). Here we successfully use the fossil record to test an ecological pattern over geological timescales, and pioneer large-scale quantitative analyses that directly link fossil occurrence datasets to terrestrial, paleo-environmental proxy data. Our results suggest that general ecological rules can neither be inferred exclusively from the geological past nor from present-day data alone. Mammalian diversity and terrestrial primary production are currently much lower than over the last 23 million years, and seem to be inconsistent with the universal diversity-productivity relationship we find through the Neogene. This renders predictions of future diversity dynamics based on knowledge of past and present relationships more challenging than previously thought. In fact, accelerating human impacts strongly decrease the probability of a rebound of diversity (8, 9, 28), supporting the hypothesis that an irreversible anthropogenic state shift of the biosphere has already taken place (29).

Materials and Methods

Mammalian fossil data. We extracted geo-referenced and dated fossil species and genus occurrences of non-marine members of the mammalian orders Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea throughout the Miocene and Pliocene for North America (30, 31) and for Eurasia (NOW - the New and Old Worlds Database of Fossil Mammals, http://www.helsinki.fi/science/now/). Original data will be publicly available through the NOW database during 2016, and our cleaned datasets, processed data for analyses, and R scripts are available online (http://dataportal-senckenberg.de/database/metacat/bikf.10018.1/bikf). Fossil locations were only included if they could be unambiguously assigned to one time interval. The sources used two different chronologies (Table S1): the North American Land Mammal Ages (NALMA) (32) and the Mammal Neogene (MN) units (33). We evaluated mammalian diversity within these land

mammal ages or units to gain a detailed view of temporal diversity dynamics, but also combined occurrence data into a set of broader, global stratigraphic stages (34) (Table S1). While these were less well resolved in time, they were comparable across continents and matched the temporal resolution of the paleobotanical data.

We followed the taxonomy of our sources for fossil (30, 31, NOW database) and extant species (35). The raw data were corrected on the species level for taxonomic errors and the taxonomy unified across the data sources, to avoid biases in genus counts due to synonyms (taxonomic look-up table available online). We performed all analyses at the genus level because the sampling bias inherent in the fossil record should be less influential on diversity estimates calculated at higher taxonomic levels (6). Additionally, morphological disparity at the genus level in fossil mammals has been shown to approximate disparity at the species level in extant mammals (36, 37). The final dataset contained a total of 1,688 unique species in 663 genera, plus 27 genera for which we had only genus-level occurrences (full dataset available online). We performed analyses at two spatial extents: continental datasets of North America and Europe included all their respective locations. For regional analyses, focal regions defined based on existing knowledge of biogeographic history (12, 19) were small enough to capture biogeographically meaningful units, but large enough to contain a sufficient number of mammalian fossil locations within the stratigraphic stages (Fig. 1, final regions delimited on a 1° latitudinal-longitudinal grid).

Estimation of mammalian γ diversity. The number of genera varied considerably across time intervals (Table S1), and was significantly correlated with the number of locations (Fig. S1; r=0.83, t=9.8, d.f.=45, $P<0.001$ across all time intervals for continents; r=0.76, t=13.3, d.f.=130, $P<0.001$ for regions). We corrected for this sampling bias with algorithms to estimate γ diversity (i.e. the region- or continent-wide genus richness) based on the occurrence of genera (20, 38-40). We applied the richness estimators Chao, Jackknife, and

Bootstrap (20, 40) to a genus-by-location matrix of presences and absences for each time interval within each focal region and each continent. From these matrices, we also calculated genus-level occupancy for each subset, i.e. the number of locations where a genus was present (36). We applied the site-specific, abundance-based richness estimators of Chao1 (the unbiased variant of the Chao estimator) and ACE (Abundance-Coverage Estimator) to these occupancy data, treating a region or continent as one site (20, 39). Analyses were performed in R with the vegan package (41, 42), and estimates based on less than six locations were excluded.

Values of γ diversity from different estimators were strongly correlated (Fig. S2A-K), so we present results with first-order Jackknife here (see *SI* methods for details of estimator selection and results with different estimators). One central issue is that diversity in the relatively long stratigraphic stages is likely to represent signals of both standing diversity and temporal turnover of genera within a stage. We were restricted to global stratigraphic stages for comparison between the two continents and because terrestrial NPP data were only available at that temporal resolution. To directly assess the effect of temporal resolution, we repeated analyses with the diversity estimates in the more finely resolved land mammal ages, which were then averaged within stratigraphic stages. Further, we assessed key assumptions and the performance of diversity estimation in supplemental analyses and simulations (following (36, 38, 43), see *SI* methods and Fig. S2-S4).

Estimation of present-day diversity and end-Pleistocene and Holocene extinctions. To estimate present-day γ diversity for the same five orders of large mammals, we extracted occurrences by overlaying species' range maps with our 1° grid (Fig. 1). We edited the range maps from the IUCN Red List Global Mammal Assessment 2008 (www.iucnredlist.org/mammals) to match our taxonomy (35) as described previously (44), excluding humans, domesticated and marine species, and uncertain, historical and introduced

ranges (see *SI* methods for details). The dataset included a total of 861 extant species in 267 genera across the globe, and 86 species in 44 genera in our regions (Fig. S7A). To adjust for the effects of end-Pleistocene and Holocene extinctions, we compiled available lists of extinct species (11, 23), selected the species recorded for our focal regions, and cross-checked them with our extant dataset (see *SI* for final list). We then adjusted present-day mammalian diversity in each continent and focal region by adding the number of extinct genera to the present-day observed genus richness.

Paleobotanical data. Paleo-climatic data were obtained from several public sources that covered the Neogene as a whole (18), exclusively the Miocene (45), or exclusively the Pliocene (46, 47). We used terrestrial estimates of mean annual temperature and precipitation inferred from fossil plant communities, which allowed us to calculate spatially explicit values of terrestrial NPP for each region or continent. We consider these datasets appropriate for the large temporal and spatial scales addressed here (48), and accounted for the temporal and climatic uncertainties associated with paleobotanical climate reconstructions as follows (see *SI* methods and Fig. S5 for details). We allocated paleo-climatic records to our stratigraphic scheme following two different approaches to account for temporal assignment uncertainty (*SI* methods), but found no substantial differences between the resulting NPP datasets (Fig. 2J, K). To account for the spatially clumped data structure (Fig. 1), we summarized the paleo-climatic records that fell into our set of focal regions (344 records in 182 locations, or 439 location-by-stratigraphic-stage combinations, available online) into the 1° grid (Fig. S5). As paleo-climatic records often provided ranges between minimum and maximum estimates that reflect climatic uncertainty for each fossil plant community (18), we took the entire distribution of climatic estimates into account when calculating mean estimates (and 50% credibility intervals) for each grid cell (*SI* methods and Fig. S5).The vast majority of paleo-climatic records were from Europe (Fig. 1). The sparseness of records in North America is

due to the known rarity of suitable preservation settings for paleobotanical material in the arid Neogene there (49), and hardly any alternative terrestrial paleo-climatic records exist for our spatial and temporal scales (50). We excluded paleo-climatic data derived from Neogene paleosols in North America (49), because these showed very low spatial and temporal congruence with our data (most paleosol data were for Central North America), and similar paleosol compilations are lacking in Europe.

Calculation of NPP from paleo-climatic estimates. We calculated NPP (in g dry matter/m^2/year) with the Miami model formula (51) (see Fig. S5B) within each of the 1° grid cells that contained an estimate of mean annual temperature (MAT, in °C) and an estimate of mean total annual precipitation (MAP, in mm/year). The Miami model is commonly applied to fossil data where no other NPP estimates or environmental drivers for more complex modelling are available, and is considered robust at large spatial scales (52). We further demonstrated the robustness of NPP estimates from the Miami model with present-day data (see below). Our methods assume no effects of temporal changes in atmospheric CO_2 levels on paleo-climatic estimation from plant fossils and on conversion of paleo-climatic values to NPP estimates, because past CO_2 levels are still under debate, and recent vegetation models suggest that they are likely comparable to pre-industrial levels since the late Miocene at least (50). Additionally, the influence of CO_2 fertilization on paleo-climatic reconstruction is considered negligible particularly in areas where water is not the main limiting factor (18). For each stratigraphic stage and each region and continent, we calculated weighted mean NPP based on all grid cells with both a MAT and a MAP estimate (excluding stages with only 1 cell). To account for uncertainty in underlying climatic estimates, we used our measure of the paleo-climatic variance within grid cells as weights, i.e. we calculated a mean that was weighted with the inverse values of the width of the 50% credibility interval from the binned distribution of original paleo-climatic estimates (*SI* methods and Fig. S5C).

Present-day NPP data and human appropriation. To obtain comparable NPP estimates for the present-day, we calculated NPP with the Miami model (51) from contemporary climate records. Data on MAT and total annual precipitation from the CRU TS dataset (version 3.21) for the years 1960 to 2010 (53) were resampled to our 1° grid. We calculated average present-day NPP within grid cells based on the arithmetic means across the 50 years (Fig. S6A), and regional and continental estimates as the average across all respective grid cells. We did not use remote-sensing data because these show actual NPP (including human impact), whereas NPP estimated from potential vegetation is more appropriate for comparison to the fossil record. To investigate the robustness of NPP estimates, we showed that the potential NPP values derived with the Miami model correlated strongly with potential NPP estimated from a dynamic global vegetation model (DGVM; Fig. S6B, E). DGVMs are sophisticated models of plant population dynamics in response to abiotic parameters, and perform well in the biomes covered by our focal regions (54); the DGVM used here was based on plant physiology, atmospheric CO_2, climate, hydrology, and soil (10). Our comparison (Fig. S6E) showed that NPP estimates derived with the Miami model provided a realistic picture of present-day potential NPP in the absence of human impact at the global scale. Finally, we estimated the actual primary productivity available in natural ecosystems today by adjusting NPP values for human appropriation of NPP (HANPP) with a correction factor (Fig. S6C), which was the proportion of potential NPP (modelled by the DGVM, Fig. S6B) that remains after human modification and harvest (10). Remaining NPP adjusted for human appropriation (Fig. S6D) was calculated for each grid cell by multiplying potential NPP from the Miami model with the HANPP factor.

Analyses of the mammalian diversity-productivity relationship. We analyzed the temporal relationship of fossil γ diversity with NPP separately on the continental and regional scales and across stratigraphic stages for which we had sufficient data (>5 mammalian

locations and >1 grid cell with NPP estimate), from the Aquitanian (starting 23 mya, Europe only) or Langhian (17 mya, both continents) to the Early Pliocene (ending 2.6 mya; datasets and R scripts available online). We fitted GLMMs with Poisson-distributed errors using Maximum Likelihood with the lme4 package for R (55). We chose a particular model structure because it best represented the hypothesis we wanted to test, i.e. whether γ diversity was related to NPP when accounting for effects of area and duration of the time interval (38) as well as for the temporal and spatial structure in the data (see Table 1, *SI* methods and Table S2 for details). These models were the best GLMMs from a selection of possible model specifications we tested (Table S2) following a standardized protocol (56). Marginal and conditional R^2 values for GLMMs were calculated with the MuMIn package (57, 58).

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Figure Legends

Fig. 1. Spatial coverage of the Neogene paleobotanical and mammalian fossil records in focal regions (black outlines): (*A*) Western, Central, and Eastern North America; (*B*) Western, Eastern Europe and Caucasus. Based on 145 paleobotanical locations (green diamonds), we estimate NPP across each continent and within each of the three best-covered regions (Western North America, Western and Eastern Europe). The coverage of 1,567 fossil locations for large terrestrial mammals is shown as the number of localities (unique combinations of spatial location and stratigraphic stage, grey shading) in 1° latitudinal-longitudinal grid cells.

Fig. 2. Temporal dynamics of Neogene mammalian diversity (*A*-*H*) and net primary production (*J*-*K*) in North America (*A, J* continent-wide, *C* Western, *E* Central, *G* Eastern North America) and Europe (*B, K* continent-wide, *D* Western, *F* Eastern Europe, *H* Caucasus). (*A*-*H*) Patterns of γ diversity for large terrestrial mammals (genus-level, first-order Jackknife estimation) are largely consistent in global stratigraphic stages (black trend line: natural cubic spline interpolation, vertical bars indicate standard errors) and continent-specific land mammal ages (red stepped line and error bars). Only time intervals with >5 mammalian locations are shown. Present-day observed genus richness (blue squares) is markedly lower than fossil diversity. (*J*-*K*) The fossil NPP estimates in the two continents within stratigraphic stages (orange and green symbols: symbol size indicates number of grid cell values underlying the estimate, error bars indicate the entire range between average minimum and maximum values across the grid cells) were very similar with two approaches to allocate paleoclimatic estimates to stratigraphic stages, i.e. whether paleobotanical records

were assigned automatically following absolute dates given in source datasets (orange) or whether they were assigned manually according to stratigraphic information in source datasets (green). Neogene estimates were generally much higher than the present-day estimates (potential NPP, blue squares with standard errors too small to see). Stratigraphic stages (see *SI*, Table S1): Aq, Aquitanian; Bu, Burdigalian; La, Langhian; Se, Serravallian; To, Tortonian; Me, Messinian; EP, Early Pliocene; LP, Late Pliocene; Pl, Pleistocene.

Fig. 3. Models of the fossil mammalian diversity-productivity relationship in (*A*) continents and (*B*) focal regions across stratigraphic stages in the Neogene (black), and visual comparison with present-day data (grey and color). Generalized linear mixed-effect models (black continuous lines) account for temporal and spatial data structure with random effects (dotted lines), and show consistent effects of NPP on fossil γ diversity (black symbols: mean conditional response values for stratigraphic stages (as in Fig. 2) predicted for median values of the fixed-effect covariates; see Table 1). Present-day data fall below the fossil model predictions (dashed lines): observed data (grey symbols), data adjusted for human appropriation of NPP (blue), and data adjusted for end-Pleistocene and Holocene extinctions (red).

Figure 1

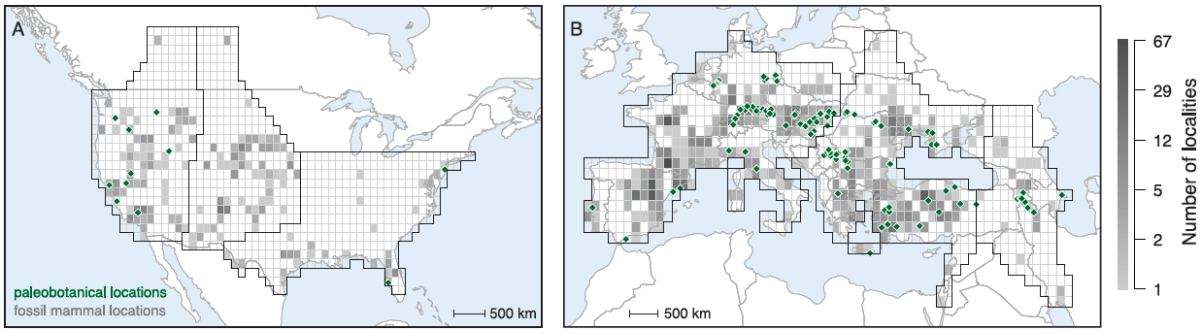

A
paleobotanical locations
fossil mammal locations
500 km
B
500 km
67
29
12
5
2
1
Number of localities

Figure 2

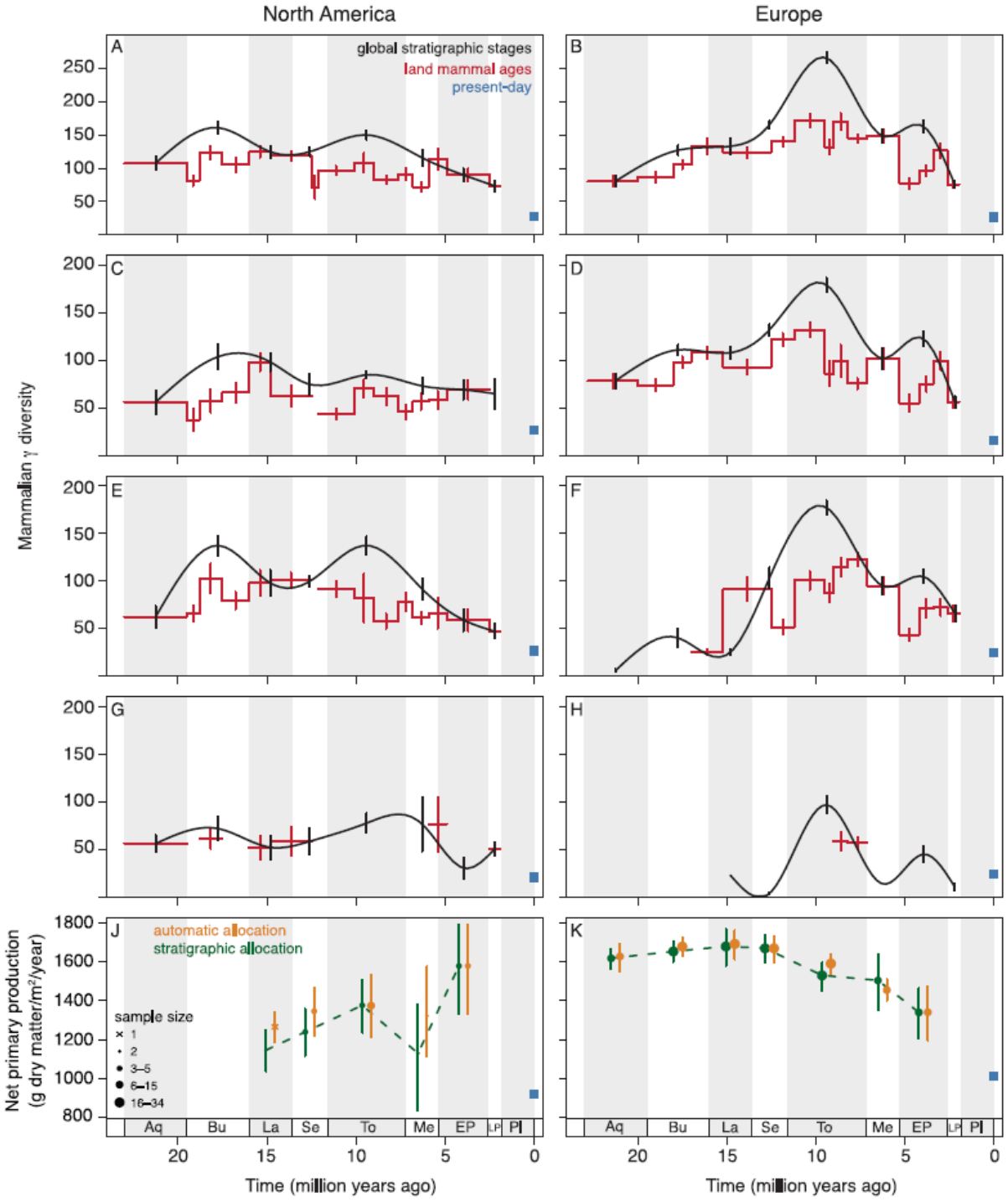
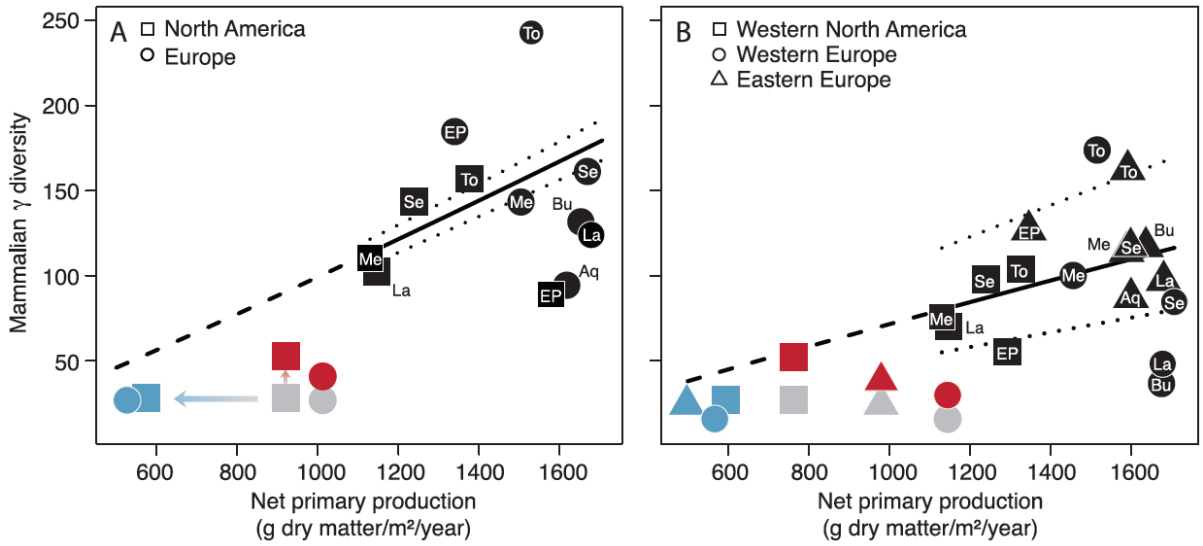

North America
Europe
A
B
C
D
E
F
G
H
J
K
global stratigraphic stages
land mammal ages
present-day
Mammalian γ diversity
Net primary production (g dry matter/m²/year)
automatic allocation
stratigraphic allocation
sample size
× 1
• 2
• 3–5
• 6–15
● 16–34
Aq
Bu
La
Se
To
Me
EP
LP
Pl
Time (million years ago)

Figure 3


A
North America
Europe
B
Western North America
Western Europe
Eastern Europe
Mammalian γ diversity
250
200
150
100
50
600
800
1000
1200
1400
1600
Net primary production
(g dry matter/m²/year)
To
EP
Se
Me
Bu
La
Aq